Temporal segregation of breeding by storm petrels *Oceanodroma castro* (*sensu lato*) on St Helena, South Atlantic

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SUMMARY.—The storm petrel *Oceanodroma castro* (*sensu lato*) complex shows considerable variation in the seasonal pattern of breeding throughout its extensive range in the Pacific and Atlantic Oceans. At several locations two seasonally separate, sympatric, populations exist, warranting recognition as separate species in at least one case. Here we report a hitherto unsuspected seasonal segregation of breeding among storm petrels on two small islets off St Helena in the South Atlantic. Egg laying occurs in two discrete periods, late March–early July ('cool season') and late September–late December ('hot season'). Most birds breed during the 'cool' season and their breeding success is substantially higher than that of those nesting in the 'hot' season. These results parallel the findings from similar studies of sympatric seasonal populations in both the Azores and Galápagos.

Sympatric breeding of temporally segregated populations of storm petrels of the *Oceanodroma castro* (*sensu lato*) complex has been well established at several locations for some years (e.g. Galápagos: Harris 1962; Azores: Monteiro & Furness 1998). Recent molecular, morphological and behavioural studies have greatly clarified taxonomic relationships amongst those populations in the Pacific and North Atlantic (Bolton 2007, Friesen *et al.* 2007, Smith *et al.* 2007), leading to the proposal to treat one such population specifically (Azores hot season: Bolton *et al.* 2008); further taxonomic revisions are anticipated. In contrast, populations in the South Atlantic have been less well studied (though see Allan 1962 for a detailed account from Ascension Island). Benson (1950) reported information obtained from local fisherman and a policeman during his visit to St Helena in January 1949, that egg laying occurred in October and November. Haydock (1954) found nests with eggs on George, Egg and Shore islands on 25 November 1952, and Stonehouse (1960) reported nests with fresh eggs on Egg Island on 14 November 1958. From a visit to Egg Island on 26 April 1959, Stonehouse (1960) reported just a single storm petrel without egg or chick, though with a freshly developed brood patch. More recent authors (e.g. Rowlands *et al.* 1998, Ashmole & Ashmole 2000, McCulloch 2004) all state that breeding occurs annually between October and December. Here we provide the first detailed information on breeding phenology of storm petrels nesting on two offshore islets of St Helena, South Atlantic, and examine breeding performance across six breeding cycles.

Methods

Study sites

St Helena (15°58'S, 05°43'W) lies 1,913 km from the west coast of Africa and *c.*800 km east of the mid-Atlantic ridge, having drifted some 150 km north-east from the hotspot on the African Plate where it was formed by volcanic activity about 14 MYA (Rowlands *et al.* 1998). The main island is surrounded by 24 satellite islets and stacks, most within 100 m of the coast and of very limited area, the largest being *c.*4 ha. Several species of predator

(domestic cat *Felis cattus*, Black Rat *Rattus rattus*, Brown Rat *R. norvegicus* and Common Myna *Acridotheres tristis*) have been introduced to St Helena since the island's discovery in 1502. Seabirds vulnerable to predators are consequently restricted to these very small offshore islets and now occupy a very small proportion of their former potential range. The present study was undertaken on two neighbouring islets, Egg Island (*c.*4 ha) and Peaked Island (*c.*0.5 ha), which lie *c.*350 m apart and less than 100 m off the north-west coast. On these islets, storm petrels nest under lava screes and in the remains of walls associated with former fortifications. Nests are often very close to the surface, the incubating bird being clearly visible. The islets also support large numbers of breeding Brown *Anous stolidus* and Black Noddies *A. minutus*. Whilst no avian or mammalian predators are resident on these two islets, Common Mynas visit from the main island and have been observed taking or scavenging seabird eggs and chicks (EB pers. obs.). Although St Helena lies well north of the Tropic of Capricorn, the climate is subtropical, with temperatures ameliorated by the south-east trade winds. The warmest month, March, is at the end of the austral summer (mean air temperatures at Jamestown, on the coast, range from 24.5–29.2°C) and the coolest month is September (19.6–23.8°C). Sea surface temperatures similarly peak in March (24.5–25.0°C) and are coolest at the end of the austral winter in September–October (19.5–21.5°C: Rowlands *et al.* 1998).

Monitoring protocols

Egg Island and Peaked Island were visited approximately monthly from November 2004 to June 2007. Nests of storm petrels were located by visual searches of suitable habitat over all parts of each islet that are safely accessible. Nests were marked with uniquely numbered tags to enable the breeding history at individual nests to be followed over the course of the three-year study period. The contents of each nest were recorded on each visit according to the following categories: adult incubating (egg present), downy chick (0–28 days), downy/feathered chick (29–49 days), nearly fledged chick (50–70 days). The approximate ages of each growth stage were assumed following Allan (1962). The approximate timing of laying, hatching and fledging was determined from the presence of incubating adults and back-calculation of laying dates from the ages of chicks assuming a 42-day incubation period from laying to hatching and a 70-day chick development period (Allan 1962, Harris 1969).

Data analysis

Daily egg and chick survival rates were calculated following Mayfield (1975) and their standard errors following Johnson (1979). The timing of egg and chick outcomes (i.e. hatch/fledge/fail) was assumed to have occurred halfway between visits (Mayfield 1975), unless the stage of development of the chick indicated otherwise. Hatching success (the percentage of eggs hatching) was calculated assuming a 42-day incubation period from laying to hatching and fledging success (the percentage of hatched chicks surviving to fledging) was calculated assuming a 70-day chick development period (Allan 1962, Harris 1969). Breeding success (the percentage of eggs laid that result in a fledged chick) was calculated as the product of hatching success and fledging success. Egg and chick survival rates were examined in relation to breeding season using a General Linear Model implemented in SAS v 9.1. Daily survival rates of eggs and chicks were modelled as a binomial response variable with the number of days exposure as a binomial denominator (see Aebischer 1999).

Results

Timing of breeding

The occurrence of incubating storm petrels on each islet showed two distinct seasonal peaks, with an absence of incubation at other times of year (Fig. 1). The estimated egg-laying periods, from timing of incubation and back-calculation for nests containing chicks, are from late March to early July ('cool' season) and late September to late December ('hot' season). The chick-rearing periods lasted from mid May to late October in the 'cool' season and from early November to late April in the 'hot' season. There was a single instance of a downy chick present in a newly discovered nest on 28 March 2006, which probably related to a late 'hot'-season breeding attempt (egg laid in January). The same nest was occupied by an incubating 'cool'-season adult when it was next checked on 25 April.

The number of nests monitored from the egg stage during each season ('hot' and 'cool') is given in Table 1. Whilst these data do not represent a systematic assessment of absolute population size, they do strongly suggest that larger numbers of birds breed during the 'cool' season (late March–late October), given the similar level of search effort in each season.

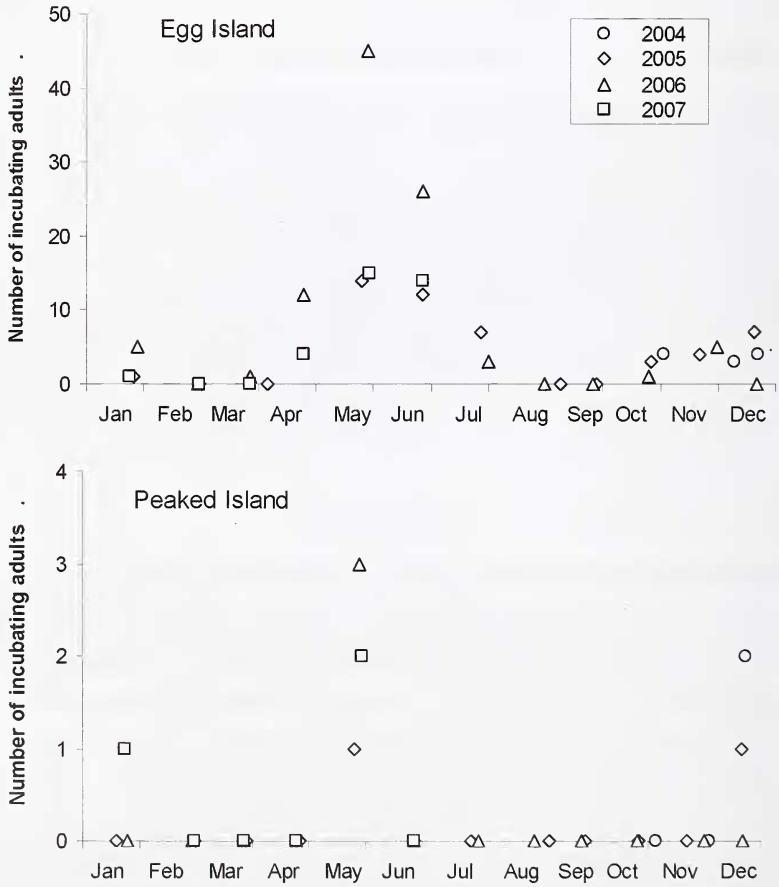

Figure 1. Number of incubating storm petrels *Oceanodroma castro* by date at Egg Island and Peaked Island, St Helena, South Atlantic, November 2004 to June 2007. Laying occurs in two distinct periods, late March–early July ('cool season') and late September–late December ('hot season'). The total number of incubated nests present at each visit is shown, so some nests were recorded on more than one visit.

TABLE 1
Number of nests monitored from the egg stage on Egg Island and Peaked Island each season.

	'Cool' season (laying March–July)			'Hot' season (laying September–December)		
	2005	2006	2007	2004*	2005	2006
Egg Island	42	87	34	13	24	12
Peaked Island	3	4	3	2	0	2

* Refers to calendar year in which eggs were laid. Note that chicks hatching from eggs laid during the 'hot' season will not fledge until the following calendar year.

TABLE 2
Daily survival rates of eggs and chicks of storm petrels *Oceanodroma castro* nesting on Egg Island and Peaked Island, St Helena, South Atlantic (± 1SE). Note monitoring ceased before the main chick-rearing period in the cool season in 2007 precluding assessment of chick survival rates.

	'Cool' season (laying March–July)			'Hot' season (laying September–December)		
	2005	2006	2007	2004	2005	2006
Daily nest survival	0.980 ± 0.005	0.979 ± 0.003	0.971 ± 0.008	0.971 ± 0.011	0.960 ± 0.010	0.966 ± 0.012
Hatching success	0.427	0.412	0.291	0.286	0.182	0.233
Daily chick survival	0.992 ± 0.003	0.994 ± 0.002		0.992 ± 0.008	0.938 ± 0.061	0.963 ± 0.036
Fledging success	0.555	0.671		0.566	0.011	0.071
Breeding success	0.237	0.277		0.162	0.002	0.017

Breeding success of seasonal populations

Insufficient nests were available for study on Peaked Island to permit an assessment of breeding success for the two islets separately, so data were pooled. Storm petrels breeding during the 'cool' season achieved higher levels of productivity than those nesting during the 'hot' season due to higher daily survival of eggs (Table 2, differences between season, all years pooled: X^2_1 =5.35 P=0.02). Although there was a slight tendency for chick survival rates also to be higher during the 'cool' season compared to the 'hot' season, the difference was not significant (data for all years pooled X^2_1 =2.45 P=0.12).

Discussion

The *Oceanodroma castro* (*sensu lato*) complex shows a diverse range of seasonal breeding patterns throughout its range in both the Pacific and North Atlantic. At some breeding locations laying occurs in a single, short season: for example on Vila Islet, Santa Maria, Azores (Monteiro *et al.* 1996a,b, Monteiro & Furness 1998). Elsewhere the laying season is more protracted, with seasonal peaks (e.g. Selvagem Grande: Mougin *et al.* 1990). At the far extreme, laying occurs in two separate seasons, with intervening periods where no laying occurs and with no interchange of individuals across seasons (e.g. Plaza Norte, Galápagos: Harris 1969; Praia and Baixo islets, Graciosa, Azores: Monteiro *et al.* 1996a,b, Monteiro & Furness 1998). In situations where seasonal segregation of populations is sufficiently ancient, genetic, morphological and behavioural differences are sufficient to warrant specific recognition of sympatric seasonal populations (e.g. the 'hot season' Monteiro's Storm Petrel *Oceanodroma monteiroi* of the Azores: Friesen *et al.* 2007, Bolton *et al.* 2008). Despite these recent advances in understanding of the seasonal nesting patterns of *O. castro* (*sensu lato*) elsewhere in its breeding range, the discovery of sympatric seasonally segregated breeding among storm petrels on St Helena was somewhat unanticipated as published data indicated that nesting occurred solely in October–December (Rowlands *et al.* 1998, Ashmole & Ashmole 2000, McCulloch 2004).

Here we have shown that in 2004–07 egg laying by storm petrels occurred in two distinct periods, late March–early July ('cool season') and late September–late December ('hot season'). These seasons correspond closely to those found on the Azores (Monteiro & Furness 1998, Bolton *et al.* 2008), but note that the application of terms 'hot' and 'cool' refer to the opposite periods since the Azores lie north of the equator.

Preliminary data suggest that, currently, substantially larger numbers of storm petrels nest on St Helena during the cool season (March–July) although historical records indicate the main egg-laying season was October–November (Rowlands *et al.* 1998), which accords with the main season for most other seabirds on St Helena (Brown Noddy, Black Noddy, Sooty Tern *Sterna fuscata* and White Tern *Gygis alba*), although Red-billed Tropicbirds *Phaethon aethereus* are reported to lay in all months (Rowlands *et al.* 1998). The waters immediately surrounding St Helena are generally characterised by low primary productivity, lacking the pronounced seasonal variation found at temperate latitudes, although more productive areas lie to the north and east, associated with the Benguela Current. It is notable that the low breeding success of both 'cool'- and 'hot'-season populations reported here is very similar to that measured in both the Galápagos (Harris 1969) and Azores (Bolton *et al.* 2004) breeding colonies. It implies early recruitment and high adult survival rates for population stability, or that these studies were carried out in years of abnormally and unsustainably low productivity.

The lack of historical records of 'cool-season' breeding by storm petrels on St Helena is curious, especially given the importance of fresh seabird eggs in the diet of the local inhabitants (hence the name 'Egg Island'). It is possible that the small eggs of storm petrels were not considered worth the effort of harvesting and so a 'cool-season' breeding population was ignored. An alternative explanation, suggested by the apparent absence of breeding storm petrels on the visit to Egg Island on 26 April 1959, is that 'cool-season' breeding has arisen extremely recently there.

Potential taxonomic implications

It is notable that all other sympatric population pairs of the *O. castro* complex show negligible levels of contemporary gene flow (Azores, Galápagos, Desertas, Selvagens, Cape Verde: Friesen *et al.* 2007), but vary considerably in divergence time (from *c.*200,000 ybp to a few tens of thousands of years). The absence of exchange of individuals between breeding seasons seems probable, as suggested by Harris (1969) for birds nesting on Plaza Norte, due to the need to schedule both breeding and feather moult into the annual cycle. Since feather moult typically takes 5–7 months to complete (Allan 1962, Bolton *et al.* 2008), even birds that fail early in the nesting season would probably be unable to complete feather moult before the onset of the next available breeding season. Clearly, more work is needed to establish rates of gene flow between the seasonal populations nesting on St Helena and to elucidate the taxonomic relationships with other populations in both the Atlantic and Pacific Oceans. The available evidence suggests that storm petrels nesting on Boatswainbird Island, Ascension, 1,296 km north-west of St Helena, breed only during the 'hot' season (laying October–December: Allan 1962). Although R. Allan arrived on Ascension in early July 1958, he did not undertake intensive field work on storm petrels until September, since it was believed very few storm petrels were breeding earlier in the year (Stonehouse 1960: 159, Allan 1962). Even so, back-calculation of laying dates of chicks found during the course of his study revealed laying occurred at six nests (of 115 studied) in May–September. In the light of the discovery of a hitherto unsuspected 'cool-season' population on St Helena, the extent of 'cool-season' breeding on Boatswainbird Island should be re-examined. Research

should now focus on the possible mechanisms relating seasonal variation in food supply, nest site availability and the evolution of allochrony.

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